The Journal of HEREDITY

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(SEE PAGE 116)

Genetics and Evolution

Birth-States of Scientists

Social Objectives of Plant Breeders

Analysis of Coat Color Inheritance in Swine

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The American Genetic Association

An incorporated organization devoted to promoting a knowledge of the laws of heredity and their application to the improvement of plants, animals, and human racial stocks

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CHINCH BUGS LEFT THE STAKE

Figure 1

The variety at the left was bred for resistance to chinch bug injury. The row of Day milo, marked by the stake at the right, was completely destroyed by this pest. Plant breeding is the most effective defense we have against many pests and diseases.

BREEDING SORGHUMS FOR SOCIAL OBJECTIVES

JOHN H. MARTIN*

CROP breeders are practical humanitarians, ever striving to improve the welfare of man and animal and to abolish poverty, want, famine and misery. Conscious of the fact that many famines of the past could have been prevented had suitable crop varieties been available, they endeavor to reduce the hazards of agriculture by breeding new varieties resistant to diseases, insects, drought and storms, cold and heat. In these endeavors, crop breeders are fully aware that their accomplishments have important social and economic aspects. By eliminating losses incident to pests and the weather, breeders help to stabilize yields and production, knowing that a well-balanced and diversified agriculture becomes established only where crops fed on the farm and those sold for cash both make uniformly good returns. The reduction in losses due to such "acts of God" as drought or root rot, by the growing of resistant varieties usually results in higher average yields per acre. If the apostles of an economy of scarcity view these increases with alarm, the breeder points out that such yields mean more efficient production and greater abundance, whereas crop failures bring poverty and want. Most crop breeders have long recognized that breeding merely for increased *yielding capacity* is not only difficult but often unnecessary. Varieties long in existence have shown a maximum capacity to yield five to ten times the *average acre yields* for the particular crops in the United States. Consequently, the improvement of acre yields has occupied a minor place in sorghum breeding as is apparent from the record of achievements which follows.

Much of the work of crop breeders has been devoted to social and humane objectives. For example, the replacement of numerous bearded wheats and rough-awned barleys with new awnless or smooth-awned varieties, although adding little to productivity, has contributed greatly to the comfort of the men and beasts who have suffered from contacts with harsh awns. A few early experiences of the writer in extracting stiff, ever-burrowing, barbed barley awns from the swollen mouths of horses and from his own eyeballs and underwear left no doubt as to the need for material improvement in that respect. Also, stiff-stalked strains of hybrid corn and other cereal crops have helped mankind by facilitating machine harvesting, thus conserving the energies and back muscles of workers who heretofore had to stoop to the ground to gather lodged crops. The breeding of cereals for improved technical quality has for its ultimate objective greater human satisfactions in the form of better bread, beverages, and other cereal products that we consume.

Perhaps the greatest social achievement of the crop breeder has been the reduction of ravages by disease. Any understanding person who has seen widespread areas of a crop devastated by a disease, and is cognizant of the blasted hopes, of the fears, poverty, and human and animal privation accompanying a crop failure cannot but hope that something be done to prevent the recurrence of such a disaster. During the past 25 years the major efforts of crop breeders have been devoted to that objective, and scores of new disease-resistant varieties now on American farms attest the success attained. Also the growing of resistant varieties helps keep down the populations of parasitic insects and dis-

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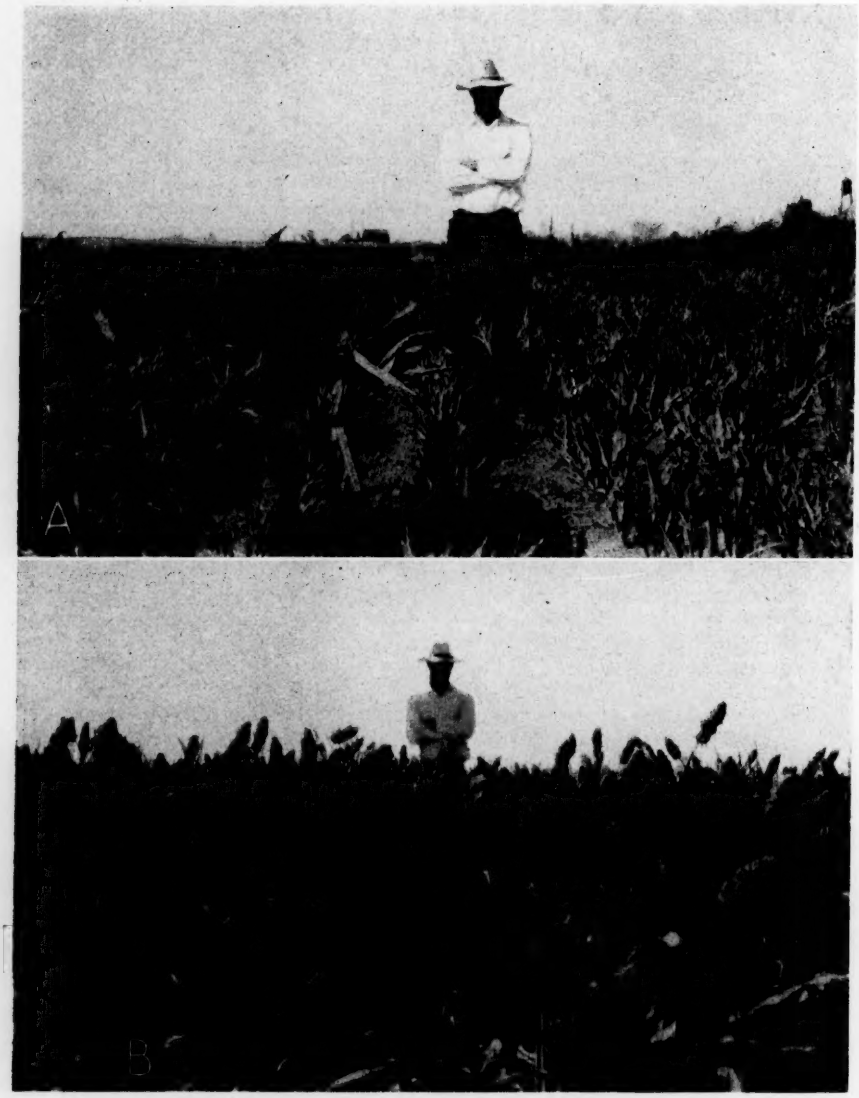


BREEDING FOR DISEASE RESISTANCE

Figure 2

A. Shows a field of ordinary susceptible Double Dwarf milo destroyed by pythium root rot. *B*. Shows a resistant strain of this variety yielding 130 bushels of grain (equivalent to 1,100 pounds of pork) per acre on an adjoining field. Where crops are grown intensively the continuing efforts of the plant breeder are essential to avoid disastrous crop failures.

ease organisms. Unless the breeding for resistance to diseases and insects goes on continuously, new diseases and pests and new strains of the older parasites, soon multiply. These have more than once created havoc among varieties that were originally resistant to attack. Consequently, the sometimes maligned crop breeder is just as essential to maintain a vitalized, intensive agriculture as the farmer who grows the crop.

The humanitarian and social benefits resulting from the improvement, since World War I, of just one crop, viz, sorghum, are reviewed here. The items mentioned are accomplishments of the Federal and State sorghum breeders* with whom the writer has been associated. The story of the improvement of many other crops would be similar.

Improved Sorghums Check Human and Animal Privation

In 1925, a new disease, now known as pythium root rot or "milo disease," was discovered in certain varieties of sorghum growing on two experiment stations. Later, this disease was found to be widespread on farms. It sometimes destroyed entire fields, as shown in Figure 2. However, the more common experience was a reduction of a third to a half in yield without the grower's being aware that a disease was the cause of his poor crop until he later tried a resistant strain. The breeding of resistant strains of all susceptible varieties has now been completed so that losses from this insidious disease are today nearly negligible. In this case the remedy was available before farmers knew that the disease existed. Livestock no longer need be undernourished because of grain shortages caused by pythium root rot.

Chinch bugs have often damaged sorghums in a drastic fashion. Some varieties were found to be much more susceptible than others but no variety is fully immune from injury. The breeding of resistant strains of susceptible types thus far has been only partly successful. However, sufficient progress has been made so that by the proper choice of varieties and cultural practices the more severe losses from chinch bugs can be avoided. The contrast between susceptible and resistant varieties is often striking as shown in Figure 1. Thus again crop research brought to the farmer and to the Nation more milk, more meat, and more wealth.

During the unprecedented drought of the 1930's, the corn crop in the Great Plains region failed with almost sickening regularity. Sorghum, which resists drought much better than does maize, was already widely grown in the southern and central Great Plains, but the varieties grown for grain matured too late for the northern sections. Fortunately, sorghum breeders to the South had anticipated the need of their northern friends before many of the latter realized it themselves. Quick-maturing grain varieties, especially for the North, were being bred in Oklahoma, Kansas, and Colorado. These new varieties were soon made available to farmers of South Dakota and Nebraska. As a result, livestock starvation and human deprivation were held in check until the drought was over. The new sorghum varieties, Sooner, Colby, Coes, Early Kalo and Day will long be remembered for their part in the salvation of drought sufferers. In one year the corn crop of South Dakota was so short that little was available for the decoration of the famed Corn Palace at Mitchell. However, sorghum was abundant despite the drought, and the exterior designs on the building were constructed of sorghum heads of four different colorful varieties. By that expedient, the cultural and social value of the annual Corn Palace fair was preserved, a curious symbol of a change in agricultural practice only possible because of foresighted scientific breeding.

*These include R. E. Karper, J. H. Parker, J. B. Sieglinger, A. F. Swanson, J. R. Quinby, J. C. Stephens, D. L. Jones, J. F. Brandon, B. F. Barnes, R. O. Snelling, W. M. Osborn, and others.

ATLAS OF THE GRAINFIELD

Figure 3

Atlas sorgho (left) stands up and is harvested readily. Kansas Orange sorgho (right) is down and tangled, a condition that adds enormously to the time and effort of harvesting.

Sorghums Bred for Machine Harvesting Save Toil

Harvesting grain sorghum by the older methods of hand topping and row binding requires extensive hand labor. Combines were never used for harvesting any crop in the southern Great Plains until 1918, and were not generally acceptable for harvesting even wheat for five or six years thereafter. It was fully recognized that the varieties of sorghum then available were too tall and weak-stalked, or had recurved heads that made them unadapted to efficient combine harvesting. Experiments were begun as early as 1919 to develop suitable varieties. Beaver, the first extra-dwarf, stiff-stalked combine-type grain sorghum variety for growing in the southern Great Plains was distributed in 1928. Other new short, erect-headed varieties — Wheatland, Day, and Colby —followed in later years (Figure 4). The greatest progress was made only recently. No less than eight new improved disease-resistant combine varieties have been distributed since 1940. About seven million acres, or 80 per cent of the sorghum harvested for grain in 1944, consisted of these new varieties cut with combines. Thus, during one war-time year when labor was virtually unobtainable, some 120 million bushels of grain were harvested by a method requiring only one-eighth of the manpower necessary to harvest the varieties available 15

years earlier. In the light of current food shortages, the social gains resulting from an additional billion pounds of meat or two billion quarts of milk cannot be overlooked.

Better than Liniment

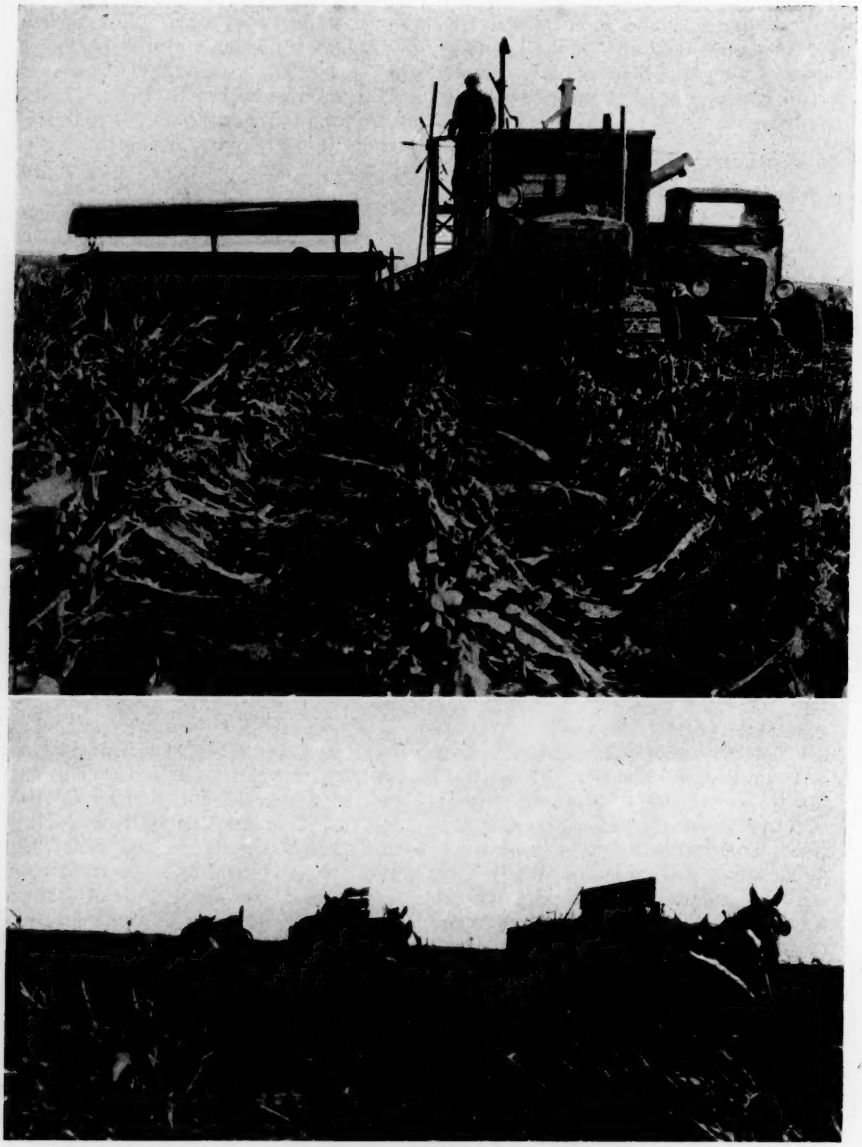
Bundles of sweet sorghum stalks cut for forage or silage are difficult to handle under the best of circumstances because of their weight and length. When the stalks fall down before harvest, difficulties are multiplied and the labor becomes back-breaking indeed. Sorghum breeders long ago felt the urge to ease the burdens of the harvesters. Their most striking achievement toward this end was the development of the Atlas variety. It has stronger stalks and is thus less likely to lodge than other sorghum varieties of similar height and growth. This characteristic, together with the palatable white seed, explains why Atlas sorgo, first distributed in 1928, soon became a leading silage and fodder crop in the area from central Kansas and Nebraska eastward. Early Kalo is a highly productive grain sorghum grown in western Kansas and Nebraska, but the stalks are so slender that they often topple over soon after the grain is ripe. The crop can be saved usually by cutting it promptly with a binder, a method entailing considerable hand labor. Sometimes, in the hope of saving labor, growers allow Early Kalo to stand until the grain is dry enough to harvest with a combine but in so doing they run a serious risk of having the crop fall down, after which the grain can be saved only by tedious hand heading of the prone stalks. In order to avoid this risk, a recently developed strain from the original Kalo variety, called Midland (Kalo 617), was distributed for growing on 20,000 acres in 1944. Midland has short sturdy stalks, making it well suited to combine harvesting. In widespread farm tests in Kansas in 1943 it was found that 99.5 per cent of the Midland stalks were still standing at the time of combine harvest. It is difficult to evaluate the social gain in terms of relief from strain and toil, as a result of the growing of stiff-stalked sorghums. Nevertheless, in total human benefits it probably excels any patented, pain-killing, snake-oil backache remedy yet devised. This is an addition to the more readily evaluated savings in man-hours during an urgent labor shortage.

Tapioca Food Industry Saved by Sorghum Breeders

Chemical tests of sorghum seeds ten years ago revealed that several American varieties had a type of endosperm described as "waxy." Later investigations by others showed that the characteristics of the starch from "waxy" cereals were similar to those of tapioca starch and that waxy sorghum starch could replace the imported tapioca starch for puddings, pie fillers, and adhesives. Many children and sick persons, especially those with sore throats, find tapioca pudding easy to take. Some years ago, Leoti, a waxy-seeded forage sorghum, was crossed with Club, a productive grain type with large, soft seeds. Some of the selections of the waxy type from this cross were productive and had grain characters that made them very satisfactory for processing. When imports of tapioca were cut off by the War, one of the strains from the breeding nursery was increased to furnish seed supplies for commercial production. The new variety, named Cody, was increased from 20 pounds of seed from the 1941 crop to a supply for processing of *32 million* pounds of grain in 1944. As a result of this one breeding activity, millions of Americans will be able to get their favorite puddings and pies while the principal tapioca-producing areas are still in Japanese hands. Here we have again a large intangible gain in avoiding dislocation of food-habits plus the dollars-and-cents and man-hours contribution of making possible the use of a food processing industry without reconversion.

New Varieties More Palatable to Animals

Like human beings, domestic birds and animals exhibit very definite preferences in their food whenever choice is



SPEEDING THE HARVEST

Figure 4

A—Three men with a combine, harvest, thrash and haul the grain from an acre of a new dwarf "combine" grain sorghum in 15 minutes, and ride all of the time. This compares with the old way (*B*) where men walking beside wagons, by the laborious "hand-topping" method, harvest and thrash an acre of unimproved tall "crooknecked" milo in about two hours. The production of varieties adapted to combine harvesting has increased the man-hours efficiency of harvesting fully eight-fold.

permitted. They distinctly prefer sorghum seeds that are white or yellow. Nearly all of the sweet sorghums and some of the grain sorghums have brown seeds with a bitter taste. Sorghum breeders have a sympathetic interest in their animal friends as well as in their fellow humans. Consequently, they began some 25 years ago to breed strains of sorghum with palatable white or yellow seeds that otherwise were equal or superior to the bitter brown-seeded varieties. Atlas and Norkan sorgo are the outstanding achievements in this respect. However, many strains of white and yellow-seeded Darso also have been developed and it is expected that one or more of these may replace the reddish-brown-seeded variety now widely grown. Whether or not livestock and poultry thrive any better on the palatable-seeded varieties has not been determined and, at present, the economic benefits seem somewhat doubtful. It seems safe to assume, however, that a tasty diet will make the animals more contented and it may well increase their food intake, assuring optimum development.

Breeders Bring Relief to Broomcorn Harvesters

Broomcorn is a specialized type of sorghum grown for the peculiar "brush," the fibrous mass of seed branches from one to two feet long. The gathering, threshing, curing, baling and handling of high-quality shed-cured standard broomcorn requires an average of 120 to 130 hours of man labor for every ton of cured brush produced. Any saving in this labor is important to the grower, particularly when help is scarce. The stalks of tall (standard) broomcorn must first be broken over or "tabled" to bring the brush within reach of the hand cutters. Dwarf broomcorn, on the other hand, is short enough to be pulled or cut directly from the standing stalk. Until recently, no dwarf broomcorn was adapted to subhumid regions where much of the high-quality broomcorn is produced, because that part of the brush enclosed in the boot usually became stained, since the boot harbors aphids and moisture. The new dwarf Fulltip variety, however, bears the brush so well exserted from the boot that little staining occurs, thus adapting it to humid conditions. Also, the improved sweeping quality of brooms made from Fulltip brush makes household tasks easier. Fulltip has been grown in central Oklahoma to a considerable extent for three years, with an appreciable saving in harvest labor at a time when men are scarce. Merely eliminating the "tabling" operation saves about five miles of walking backwards while breaking over 125,000 stalks, for every ton of cured brush produced. Some 20,000 acres of Fulltip will be grown in 1945. Total drudgery done away with by this rather minor exercise of the breeder's art is equivalent in the 1945 crop to one man's walking backward around the earth at the equator. The elimination of this rather uncomfortable procedure would seem to be a definite social gain.

The chaff enclosing broomcorn seeds bears numerous hairs that rub off readily while the brush is being harvested, hauled, and threshed. These plant hairs, which cloud the air around the thresher, are extremely irritating to the eyes and nostrils and to a perspiring skin. Scratching to relieve the so-called "broomcorn itch" often causes considerable areas of the skin to become infected. Then complications set in. "Broomcorn Johnnies," as itinerant broomcorn field hands often are called, regard the "itch" as the most objectionable feature of their job. To remedy this situation, broomcorn was crossed with a brushy-headed sorghum from China that had little fuzz on the chaff. Subsequent recrossing and selection produced a broomcorn that, if grown widely on a commercial scale, should largely eliminate irritation from the hairs. Then the "gripes and groans" of the "Johnnies" should likewise be largely eliminated. When such varieties have come into general use the alleviation of human misery will have been brought one step further.

Even "Plenty of Nothing"

Not all crop improvement results in

increased yields. Many disease-resistant varieties yield no more than the varieties they replaced, except when the disease is present. They merely stabilize yields at a satisfactory level. Some improved varieties having better quality, shorter or stiffer stalks, or other desirable characteristics yield even less than the varieties they replaced. Thus, Atlas sorgo yields less forage than Kansas Orange, the variety it has almost entirely replaced. The new combine-type grain sorghum varieties all have a lower maximum potential capacity and some of them show lower average yields than the Dwarf Yellow milo which they have replaced. All of the new quick-maturing varieties for the North have small plants and are inferior to the older standard varieties in their ability to produce under long-season, favorable growing conditions. Thus it becomes evident that some of the most important steps in sorghum improvement have come from the development of varieties with lower potential yielding ability. That, perhaps, is as it should be because the chief complaint regarding certain forage varieties is that they yield so much that they are hard to harvest. Sorghums introduced from the tropical regions all grow too large for harvesting with existing modern machinery, and thus are unacceptable here. The aim of maximum efficiency under given conditions of climate and other factors must not be lost sight of by the modern plant breeder, who tailors his varieties to order.

Breeding varieties merely for low yields has not been beyond the demands placed on the modern breeder. To meet a special situation a need arose for a sorghum that would yield nothing at all worth harvesting. When sorghum is planted on land to prevent soil blowing or to furnish a protective cover while grass is being established, it is desirable that the entire growth be left on the land. If the plants bear products that can be utilized as grain, as forage, as sirup or broomcorn brush, there is a strong urge to gather at least a part of the crop, especially when nobody is watching. The demand for such a specialized protective crop has been met by selection from a cross between Sudan grass and an inferior-quality cross-bred strain of broomcorn. The new "no-yield" sorghum removes the temptation to harvest because the stalks, although making a good growth, are too hard and dry for forage purposes and they contain no sweetness. Furthermore, the seed is too small and sparse to make it worth harvesting for grain, and the brushy heads are unsuitable for making brooms. Neither is it safe to pasture the crop because of the possibility of "sorghum poisoning" from the presence of prussic acid. Such a variety that yields merely "plenty of nothing" cannot contribute to crop surpluses. However it is available when circumstances warrant its use.

Conclusions

The examples just cited show that some of the major accomplishments in crop breeding have been directed toward human betterment and humane achievements, without having contributed to crop surpluses. In stabilization of yield through elimination of crop failures they have made a very important contribution. Furthermore, the record of achievements and objectives demonstrates that, in large part, breeders have been fully conscious of their obligation to strive for the advancement of social welfare throughout the globe.

STATES OF BIRTH OF AMERICAN MEN OF SCIENCE

RICHARD ASHMAN
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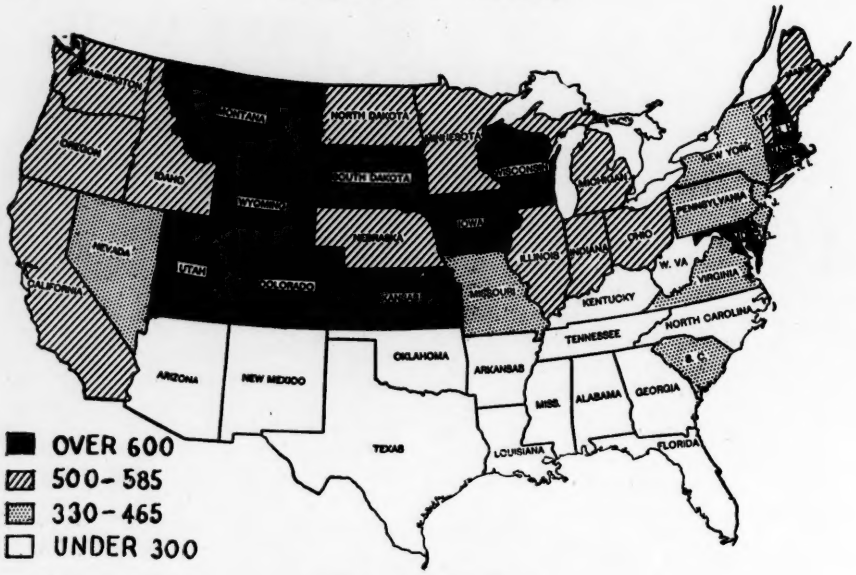
RECENTLY I listed about half the names in the 1938 edition of American Men of Science according to state of birth. I am sending in the results with the thought that some of the readers of the JOURNAL OF HEREDITY may be interested. All the starred scientists were included; their regional distribution was the same as that of the larger number, except that New England was in the lead. This was due to the greater average age of starred individuals in New England than in the West. The number of scientists born in each state was divided by the white population at the approximate time of their birth. In order to make the comparisons significant the population of each state was calculated as follows: The sum of 70 per cent of the 1870, 80 per cent of the 1880, 90 per cent of the 1890, 100 per cent of the 1900, and 40 per cent of the 1910 populations was found, and this sum was divided by 3.8. This procedure was based on the reasoning that some of the older scientists had died, and on the assumption that only about 40 per cent of the scientists born after 1900 would be included in the 1938 edition. The results differ only moderately if the 1890 populations are used instead.* The table gives the number of scientists listed for each state and the number per million of the white population. The range given is not a standard derivation or a probable error.† There is not one chance in a hundred that the true incidence falls outside the range as shown.

It may be noted that the rates are reasonably reliable only for the more populous states. Yet Utah and Colorado must be very high, whereas the real standing of Wyoming and Montana is doubtful. However, since the latter states are in a high region, it is unlikely that their true rates are as low as the average. From the regional distributions it may be inferred that Idaho and Nebraska are a little higher than the table shows, and this may also be true of Nevada and North Dakota.

A map showing the distribution of incidences demonstrates that there is a "high" in New England, centering in Massachusetts. This stretches westward across upper New York and Pennsylvania, extends farther westward south of the Great Lakes, probably crosses north-central Illinois, and then fans out, being broadest at its Rocky Mountain end where it culminates in the Utah "high." Outside of this area only Maryland and the District of Columbia constitute an elevated oasis. It was found that the rate of northern Pennsylvania (settled from New England) was about double that of the southern half of the state. This confirms the impression of a high zone, contiguous with, and stretching westward from, New England. Although not separately tested, it is likely that southern Ohio, Indiana, and Illinois are lower than their northern portions.

*If the 1890 census is used, the relative positions of Oklahoma and Idaho would be much improved, whereas the ranks of Nebraska and South Dakota would be lowered. Some of the mining states may have had a large excess of males over females, and consequently their standings as shown will be lower than the true figure. There are uncertainties with respect to a number of factors, yet the larger regional differences are undoubtedly valid. The only really accurate method of making the comparisons between states would be to use the ratio between the number of scientists born per decade in each state and the number of children born, after correction for infant mortality differences.

†It is based on an adaptation of a method used by PEARL, R., *Med. Biometry and Statistics*, page 331.



BIRTH DISTRIBUTION

Figure 5

Concentration per million population of American scientists with respect to state of birth. Climate, educational and economic opportunities differ so greatly throughout the country that these differences cannot be attributed mainly to genetic differences.

What Conditions the Differences?

The factors which may be responsible for the high zone are education, climate, genetic lines, and economic opportunity. Probably all these are involved. Yet it may be argued that heredity is largely instrumental in determining both education and also opportunity for education and employment. With respect to heritage, it is suggestive that all the way from New York to Kansas there is an apparent positive correlation between the incidence of scientists and the frequency of occurrence of New England place and family names. The historical record is clear in proving that many families of New England descent entered Utah and Colorado. In Utah, the Mormons promoted both education and large families, and there may have been other eugenic influences. The New Englanders were not in any way unique, but they were originally a selected group, which included little mental subnormality. Where, as in Utah, this stock has perpetuated itself, its high average may have been maintained. It is significant that a majority of Utah's scientists bear British names, probably from New England for the most part.

In the South the climate is a depressant. Furthermore, the South is, or is assumed to be, greatly handicapped by the aftermath of the Civil War, by differential freight rates, and other things. Yet it is difficult to escape the impression that the hereditary mean is not so high as in the Mid-West, although, of course, the highest ability in the South is as good as the best anywhere. Both in a study of the distribution of persons listed in the 1912-1913 edition of *Who's Who in America,* by Ellsworth Huntington, and in this study of scientists, South Carolina stands well above the level of the rest of the Deep South. This superiority has no relation to climate, wealth, or other obvious factors. In proportion to area and population, the state has more colleges, founded before 1891

and surviving, than any other southern state. This interest in education probably reflects the caliber of its people. Yet the colleges are impecunious, and to obtain a good education the student must often go to some other state. Huntington's conclusion was that genetic factors accounted for South Carolina's superiority, and the historical evidence appears to support this.

It is difficult to evaluate the probable genetic level of the South. In Huntington's study* the southern states of Louisiana, Mississippi, Alabama, Georgia, and North Carolina stood at about 70 per cent of the western level. Historical considerations suggest that this may be close to the actual difference. If so, then, when education and opportunity in the South equal those in the Mid-West, the South's level in the table should rise to about 450, and South Carolina should be "high"—climate permitting. In support of the genetic argument, the rank of Missouri is pertinent, when considered along with that state's history. This argument throws into relief the wastage of scientific and other potential which was due to southern environmental factors. Both Texas and North Carolina have significantly improved their relative positions in the South since Huntington's study. This may very possibly reflect the establishment in these states of the best southern state universities.

The striking changes which have occurred in the 26 years from 1912 to 1938 are the decline of New England and the rise of the Middle West and the Mountain States. These changes are due to the dilution of the New England population by recent immigration, limitation of family size, and improvement in the educational and other opportunities in the West. The relatively low level of Pennsylvania and New Jersey can be attributed, at least in part, to more recent immigration. Whatever the inherent quality of that immigration may have been, at the time of birth of most of the scientists it had not had time to prove itself. In this connection Charles A. and Mary R. Beard's recent *Basic History of the United States* gives some interesting generalizations.

Record of Newly Arrived Groups

That the national origin of the immigrant is not the important factor is sug-

TABLE I. Birth-States of 15,797 American Scientists.

State or District	Number of Scientists	Number per million of population
Utah	145	1185 ± 250
District of Columbia	116	1155 ± 280
Colorado	195	890 ± 160
Massachusetts	1024	775 ± 60
South Dakota	116	705 ± 165
Wyoming	25	705 ± 370
Montana	61	695 ± 230
Connecticut	297	665 ± 100
Iowa	687	635 ± 65
Kansas	413	610 ± 75
Maryland	321	610 ± 80
New Hampshire	134	610 ± 135
Wisconsin	584	600 ± 60
Indiana	729	585 ± 50
Maine	225	580 ± 95
Minnesota	416	575 ± 70
Nebraska	262	575 ± 90
Ohio	1162	570 ± 40
Vermont	113	570 ± 130
Idaho	35	560 ± 210
Washington	115	540 ± 125
Oregon	97	540 ± 140
North Dakota	58	520 ± 175
Michigan	581	510 ± 50
Illinois	1118	505 ± 40
California	350	500 ± 65
Rhode Island	94	465 ± 120
New York	1604	445 ± 30
Delaware	34	405 ± 165
Pennsylvania	1190	400 ± 30
Missouri	540	385 ± 40
Virginia	273	385 ± 55
South Carolina	135	380 ± 75
New Jersey	294	350 ± 50
Nevada	10	330 ± 260
Oklahoma	69	285 ± 85
North Carolina	188	275 ± 50
Arizona	13	270 ± 190
Canada	765	265 ± 25
West Virginia	109	260 ± 65
Mississippi	89	250 ± 75
Texas	266	240 ± 35
Kentucky	200	205 ± 35
New Mexico	19	195 ± 120
Louisiana	79	190 ± 50
Tennessee	145	175 ± 40
Alabama	98	175 ± 50
Arkansas	75	170 ± 50
Georgia	107	160 ± 40
Florida	22	130 ± 70

*Huntington, Ellsworth. *Civilization and Climate.* Yale University Press. 1924.

gested by other observations. The Germans and Scandinavians, at least in the Mid-West, have done well, although they were probably not so rigorously selected, for the most part, as the New Englanders. The Pennsylvania German have also done well, although data are not available to estimate how well. The incidence of scientists among the Jews appears to be high; and this may be true also of the Armenians. In view of the achievements of such unlike groups, the lower ranking of certain others may be attributed to two factors. These are both differential immigration and also dysgenic factors which operated in the countries from which these immigrants came, such as the draining off of ability by wars and into celibate orders.

Since many dysgenic factors are operating in the United States today, it is pertinent to inquire whether our civilization can long endure. For its perpetuation many things are, of course, necessary, including education. But how long shall we have a sufficient supply of educable material? No amount of social and economic reform, however desirable and necessary these may be, can prevail against a downward genetic trend, even though moderate. Civilization in the region or nation which reverses this trend may soon surpass that of the rest of the world.

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CITRUS CYCLOPEDIA

THIS volume,* the first of a trilogy on oranges, grapefruit, lemons and their kin, is not only authoritative; it is monographic in its completeness and democratically interesting. Such an unusual combination should make it invaluable to anyone at all curious about *Citrus* and its relatives. The volume under review is the most technical of the trilogy. Volume II will deal with the production angle; while Volume III will describe harvesting, marketing and utilization. Each volume is complete in itself, and all three are published as a part of a plan to celebrate the 75th birthday of the University of California. I can think of no more fitting way to honor an anniversary, for this birthday gift will benefit all humanity through centuries to come. Practically anything one would like to know that is known about the botany, breeding and history of Citrus and its relatives is to be found somewhere in this volume, and there is a good index to help one find it, and a very complete bibliography.

Today oranges, lemons, grapefruit, and limes are very commonplace fruits in American markets and are such serious competitors of fruits of the rose family as apples, pears and plums that the cash value of the citrus crop far exceeds the value of any other fruit crop. This has been true only a short time, most of these developments having taken place within the last half century, beginning about the time Drs. Webber and Swingle emerged from the college world of Nebraska and Kansas to begin their far-reaching studies on this group.

As depicted by Dr. Webber in the first three chapters, the citron, the lemon, the sour and sweet oranges, the grapefruit, and the lime have traveled a long road in order that they might take such a prominent place among us. In these chapters, the history and development of the citrus industry is traced, the various characteristics of *Citrus* species in relation to climate are described, and detailed factual information is presented concerning the commercial citrus regions of the world from a physiographic, climatic and economic standpoint.

For a very long time, perhaps up to the Tenth Century, the citron was about the only citrus fruit the western world knew. In southern Europe, far removed from its original home, man learned to candy it in the form so well known as a fruit cake ingredient. The original home of the citrus group is believed to be southeastern Asia; although Dr. Swingle thinks the citron may have been a

*The Citrus Industry, Volume I. History, Botany, and Breeding. H. J. Webber and L. D. Batchelor, Editors. Pp. 1028. 233 figures. $7.50. University of California Press, Berkeley, 1943.

native of some wild, isolated Arabian oasis.

With the rise and spread of the Arab civilization in the Tenth Century, followed by the Crusades, the sour orange, the lemon, and the shaddock or Adam's apple began to appear in Europe's fruit basket. Perhaps as much as five centuries later the sweet orange arrived over the Genoese trade route; and finally, in modern times, the tangerine or mandarin orange, the lime, the kumquat, and the grapefruit. The latter was first described from the West Indies as the "Forbidden Fruit" and may possibly have originated as a sport or mutation from the shaddock; although there is some difference of opinion regarding this.

The demand for citrus fruits in Europe created greenhouses, at first called orangeries. Citrus fruits reached America on the second voyage of Columbus in 1493 and are first mentioned in connection with continental America as having been planted in Mexico on July 12, 1518. Prior to 1739, the missions of California grew oranges, and Florida had them by 1565. Commercial citrus growing developed at about the same time in both states. Grapefruit culture, as an industry, originated in Florida, and the earliest shipments to New York and Philadelphia are said to have netted the growers about fifty cents a barrel. Citrus growing now forms a belt around the world. Tables show the world production by countries, number of trees, acreages, exports, etc.

Chapter IV is a monographic treatment of all the cultivated *Citrus* species, their near and not too distant relatives, and the known and suspected hybrids between them. Dr. W. T. Swingle has done the world a very great service in making this section an intelligible and interesting part of this book. So often such treatises are hidden away in special volumes, far out of reach of most of the people who would be interested in them. In this case, the remarkable treatise on *Citrus* systematics is part of the family circle. Here one learns first hand about tangelos, citrumquats, citranges, citrumelos, citrandarins, citremons, citrumquats, citrangedins, tangors, and yuzus, and about a dozen other little known species or generic hybrids. One of the amazing generalizations about the citrus group is the remarkable crossability exhibited. One wonders after reading about these hybrids what the commercial citrus fruits might be like a century hence. Already the hybrids are infiltering our markets under ordinary varietal names, such as "Temple." Another striking generalization from Swingle's contribution is the enormous range of variability available, a huge reservoir of potentially valuable characters as yet little utilized.

Chapter V calls the roll of the varieties, groups them into types, and gives something of their history. It is here one learns about the varieties that form the basis of the commercial industries in various parts of the world. In America, the two most commonly grown orange varieties are Washington Navel and Valencia; while among grapefruit varieties, the Marsh Seedless and the pink-fleshed Ruby are becoming very popular. As with most widely cultivated fruits, hundreds of varieties of citrus fruits exist, but relatively few of them are grown commercially.

E. T. Bartholomew and H. S. Reed, in Chapter VI, describe and discuss the structure and function of buds, leaves, flowers, fruits, trunks and roots; while in Chapter VII, H. D. Chapman and W. P. Kelley take up the mineral composition and plant-food requirements of citrus, with special emphasis on the effects of deficiencies and excesses, the effects of soil reaction, and the influence of nutrient variables on fruit quality.

In Chapter VIII and IX, H. B. Frost describes, with a minimum of technical terms, seed reproduction, the development of pollen, pollination and fecundation, selfing, crossing, pollination and fruit yields, polyembryony, seed variability, and various other seed characteristics, including germination; sterility in its various aspects, cytological methods for citrus, chromosome number, environmental and heritable variations; citrus breeding bases, procedures and techniques; naming of new varieties and the

progress and accomplishments of modern citrus breeding.

Most cultivated varieties of *Citrus* and many of their wild relatives are diploids with a haploid chromosome number of 9. When triploids occur, they seem to originate only as gametic seedlings; while tetraploids arise as nucellar seedlings, or more rarely, in stem growing points. Both triploids and tetraploids in *Citrus* show characteristic differences in tree and fruit in contrast to diploids. Tetraploids, for example, have broader and thicker leaves, thicker thorns, are slower in beginning to bloom and in fruit setting, and are more susceptible to disease. The fruits have thicker rinds, tend to color later, lose their juice earlier, are more irregular in shape, and are smaller in size.

Polyembryony in *Citrus* is very common and a source of much confusion to the plant breeder; since it involves more than one embryo in a seed, and these may be either sexually or asexually produced.

The final chapter is by A. D. Shamel, in which he discusses the problems of bud variation and bud selection as applied to commercial citrus culture. A special section is devoted to the various types of bud variations in the Washington Navel orange, such as unproductive strains, dry fruit strains, and Australian strains. Emphasis is placed on the necessity for organized bud selection work in citrus growing.

I am tempted to call this work *Encyclopedia Citrusica.*

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Frequency of Multiple Births

Early in the 19th century investigators became interested in the numerical proportion between singletons, twins, triplets, quadruplets and quintuplets. Sicklet (1859) analyzing 17.7 million births, found one pair of twins per 83 deliveries, one set of triplets in 8,077, and one set of quadruplets in 385,499 deliveries. Veit's (1855) figures were close to Sickel's (1:89 and 1:7,910). Also Wappaeus' (1859) figures showed a certain regularity in the numerical proportion of singletons to twins and triplets (1:86, 1:7,400). Apparently D. Hellin (1895) was the first to realize the rule behind that regularity. If $B/T = n$, where B is the total of births and T the corresponding number of pairs of twins, then n indicates the number of births per one pair of twins. The statistical studies disclosed the fact that if $1:n$ is the proportion of one pair of twins to n births, $1:n^2$ gives the proportion of one set of triplets to the number of births, $1:n^3$ represents the number of births among which one set of quadruplets is to be found, and $1:n^4$ gives the number of births corresponding with one set of quintuplets.

Hellin's book was not obtainable, therefore I must rely on the authority of H. H. Newman in the assertion that Hellin formulated these proportions in terms similar to those just mentioned. Apparently Hellin's law was forgotten and rediscovered 25 years later by C. Zeleny. Since then, the law has been checked and tested several times. Some authors, among them Greulich and Guttmacher, expressed themselves in favor of the rule, while others, among them R. Pearl have been rather inclined to discard the Hellin-Zeleny law on account of small deviations of the actual figures from it. How small these deviations are may be shown on U. S. A. statistics for 1939/1940. In these two years, 4,620,000 children were born, among them 49,884 pairs of twins, giving thus a proportion of 93:1; n being 93, the total number of births (B) divided by n^2 and n^3 respectively, indicates the number of expected sets of triplets and quadruplets, namely 535 and 6 respectively. The actually recorded figures were 521 and 5. Considering that sets of multiple births in which all individuals were stillborn have not been recorded, the deviations from the rule are surprisingly small.—S. PELLER. *Bul. Hist. Med.* 16:366. 1944.

GENETICS OF MACRO-EVOLUTION

A Review

MANY geneticists have had the mildly annoying experience of being told that their science, though perhaps accurately describing the events taking place in the bottles on laboratory shelves, has little relevance to the grand process of evolution. Experiments are made on relatively few individuals and are limited to few generations. Nature, so runs the argument, operates with countless individuals and eons of time. Evolution may, then, be governed by forces about which geneticists have not an inkling. One could, of course, reply that even laboratory experiments can, if necessary, involve a great many individuals and generations (e.g., in bacteria), that long-time processes should be discoverable through experiments conducted with enough precision, and that needless multiplication of unknowns is not sound scientific procedure. But after all is said and done, we cannot make a Drosophila evolve into a housefly, still less into an elephant. Changes observed by geneticists are mostly on the infra-racial, and nearly always on the infra-specific level. Only in the very special case of polyploidy can we witness what amounts to the origin of new species.

Milk Bottle to Millenium

Genetic analysis is directly applicable only within the limits in which the organisms concerned can be hybridized. Beyond these limits a geneticist can proceed only by inference. It is merely to describe this obvious limitation that this reviewer has, in an unguarded moment, used the rather unfortunate words "micro-evolution" and "macro-evolution." These words acquired wide currency when Goldschmidt used them to express his idea of a fundamental dualism of evolutionary processes. According to Goldschmidt, macro-evolution is caused by his hypothetical "systemic mutations," which give rise to fundamentally new types subsequently modified only in detail through the micro-evolutionary mutations familiar to geneticists. Anyway, micro- and macro-evolution seem to have become firmly established in the scientific lexicon.

Genetics studies the mechanism of heredity and variations. Some of these mechanisms are known to be capable of producing evolutionary changes on at least the micro-evolutionary level. This is the basis of the working hypothesis according to which whatever evolutionary processes have taken place in the history of the earth were caused by the same mechanisms. However, the body of data collected by geneticists only rarely permits inferences to be drawn regarding the historic course of the evolutionary events. The historic records are collected and interpreted by paleontologists. It is up to paleontologists to describe the actual phylogenetic transformations, and to supply the data that would permit us to test the ability of the known genetic mechanisms to account for the historic evolution, especially that on the macro-evolutionary level. For years the geneticists hoped to obtain such data from their paleontological colleagues. Indeed, they vaguely suspected that some relevant data may be already available in the paleontological literature and in paleontological museums. However, no geneticist was or is enough at home in paleontology to be able to locate the data, and no paleontologist was familiar enough with genetics to judge which data are relevant.

Such a paleontologist has appeared in the person of Mr. G. G. Simpson. His book* essays the long awaited synthesis of paleontology and genetics. Simpson is more than anybody else aware of the difficulties of the venture: "For almost every topic discussed in the following pages the data are insufficient. The student who attempts interpretations under these circumstances does so in the face

*SIMPSON, G. G. Tempo and Mode in Evolution. Columbia University Press, Biological Series No. 15, XVIII + 237 pp. Price $3.50. New York, 1944.

of certainty that some of his conclusions will be rejected." Those who delude themselves into believing that they propound only "absolutely proven" conclusions will be dismayed at the following statements: "It is, however, pusillanimous to avoid making our best efforts today because they may appear inadequate tomorrow. Indeed, there would be no tomorrow for science if this common attitude were universal. Facts are useless to science unless they are understood. They are to be understood only by theoretical interpretation." Among the latter category there are many kinds of books—some "bad," others "good."

There are simply good books. And good books which mark the end of one and the beginning of another period in the development of a given science. Simpson's book belongs to the latter class. No matter how many of his interpretations will require correction in the future, from now on no competent discussion of the mechanisms of macro-evolution can be made outside the ambit of Simpson's analysis. The gist of Simpson's book can be summarized in the following very simple, although negative, statement: paleontology has brought to light no facts that would demand the assumption of forces and mechanisms other than those dealt with in modern genetics. It is difficult within the space of a review to convey a fair idea about the contents of Simpson's book beyond the above statement, which, of course, does not begin to do it justice. The author has condensed in 215 pages the discussion of several topics each of which could well be the subject of a separate book of at least that size. One is tempted to suggest that a much enlarged edition with a more extensive documentation would eventually be in order. The following paragraphs are, then, intended merely to stimulate the interest of prospective readers.

Gaps in the Record

Accidents of fossilization can not account for some gaps in the paleontological record. Thus, every one of the 32 known orders of mammals appear in the record suddenly, "the earliest and most primitive known members of every order have the basic ordinal characters, and in no case is an approximately continuous sequence from one order to another known." The absence of transitional forms between orders, classes, and phyla is equally striking among vertebrates, invertebrates, and plants. It has been noted by many paleontologists, some of whom have seen fit to ascribe the gaps to special macro-evolutionary (or "mega-evolutionary") methods of descent. The masterful analysis of the problem by Simpson brings out the following: (1) The earliest known representatives of each mammalian order are smaller in body sizes than the average for the later representatives of that order. One may, then, infer that the missing forms (if they existed) were small animals. (2) The appearance of a new order (and, *a fortiori,* of a new class or a phylum) represents the emergence of a major adaptive novelty compared to the probable ancestors. The emergence of such novelties may entail ecological crises. (3) "The ancestral type, at the probable time of origin, is often well recorded and representative of probably abundant and widespread groups, while the first representatives of the new type are usually rare as fossils." The transition types are probably rarer still. (4) A few forms transitional between major groups are known—e.g., Archaeopteryx bridging the gap between reptiles and birds. (5) The appearance of new groups frequently, though not invariably, coincides with geological crises of mountain formation and land emergence; geological crises are likely to be accompanied by ecological ones. The missing transitional types were, then, very likely rare organisms evolving at higher rates than either their immediate ancestors or their descendants. The most favorable conditions for rapid evolution are, however, created precisely in species subdivided into numerous colonies with intermediate to small effective populations living in shifting and ecologically complex environments. Other things being equal, rare species are most likely to have small

effective populations and least likely to be preserved as fossils. "In summary, the theory here developed is that mega-evolution normally occurs among small populations that become preadaptive and evolve continuously (without saltation, but at exceptionally rapid rates) to radically different ecological positions."

The problem of rates of evolution is subjected to a penetrating analysis. Geneticists will be particularly interested to find estimates of the absolute time intervals which certain evolutionary transformations have taken. The rates of evolution vary greatly in different lines of descent. Simpson shows, however, that this variation does not conform to a normal probability distribution. Within a large group, such as an order or class, a great majority of the phylogenetic lines evolve at certain modal rates (horotelic lines), with a minority developing much more slowly (bradytelic lines), and a small minority evolving very rapidly (tachytelic lines). The evolutionary rate does not necessarily remain constant within a given line. Tachytelic lines either die out or reach new adaptive peaks and become horotelic or bradytelic; horotelic lines bud off bradytelic or tachytelic ones or vice versa. Simpson is properly sceptical about differences in mutation rates accounting for such variations in the tempo of evolution. An explanation is to be looked for elsewhere. Bradytelic forms are usually well adapted to and very common in their special environments. Their genetically effective populations are presumably large; under such conditions natural selection becomes the controlling conservative factor which destroys all departures from the norm and thus arrests the evolutionary development. Tachyletic forms have the opposite characteristics; a temporary relaxation of selection permits reaching a slope leading to a new adaptive peak, and this is followed by intense creative selection until the summit of the peak is reached.

Back to Earth

Paleontologists and comparative morphologists have been preoccupied for decades with macro-evolutionary phenomena that strained the ingenuity of geneticists to account for them without assuming other than the known principles of genetics. Theories of orthogenesis, aristogenesis, programme evolution, and the like, asserted that related groups of organisms evolve along parallel lines, as though impelled by some inner drive; that this determinate progression develops a momentum which may become deleterious to the organisms involved and lead to their extinction; that stages analogous to youth, maturity, and old age of an individual may be apprehended in the phyletic histories of groups of organisms. It is a real pleasure to follow Simpson's analysis of the pertinent facts and theories. It would not be fair to say that Simpson is doing here merely a good debunking job; he separates the grain from the chaff and shows that several different phenomena, none of them particularly mysterious, are being confused.

It should be amply clear from the preceding paragraphs that no geneticist interested in evolutionary problems can fail to study Simpson's book.

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FLOWERLESS CASTOR-BEAN PLANTS

WAYNE E. DOMINGO*

PRODUCTIVE AND FLOWERLESS PLANTS

Figure 6

General view of the F_2 population of cross 3 and its reciprocal. Plants on the extreme right are similar to both parents and F_1 in earliness of flowering (in June, at the sixth to twelfth node) and in height (four to six feet). The taller plants, constituting eight per cent of the population, were still flowerless at the time of the first freeze on October 16. This is the same general appearance presented by fields planted with seed produced for several generations by open-pollination in unisolated plots.

CERTAIN populations of the castor-bean plant, *Ricinus communis* L., long have been observed to include individuals which fail to produce flowers in temperate climates. In 1902 Shaw[1] wrote of this species under Oklahoma conditions, "Some of the plants produced no seed at all, not even flowers, while others, growing under what would seem to be exactly the same conditions, produced large quantities of seed." Such individuals have appeared in plantings of many of the so-called varieties which have been collected for observation at the Plant Industry Station at Beltsville, Maryland. Within the domestic strains, most of which contain smaller numbers of flowerless plants than those of tropical origin, the proportion of such plants has been observed to be greater in the more heterogenous material. It has repeatedly been observed when relatively pure-breeding strains were grown in adjacent plots, that the succeeding few generations grown from open-pollinated seed contained progressively greater proportions of flowerless plants. No such plants have occurred in pure-breeding adapted varieties or in the several S_3 lines which had their origin in strains with many flowerless plants. Most of the mixed seed lots from Haiti, Cuba, and Brazil, when planted in this country, produce plants which either are flowerless or blossom too late for seed to mature.

These unusual plants are undesirable from a commercial standpoint not only because they are non-producers but also because their presence indicates a degree of heterozygosity which usually complicates such production operations as planting, harvesting, and hulling.

Flowerless plants have often been designated as "hybrids." It has been the experience of White[2] and of the

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TWO SECOND GENERATION PLANTS

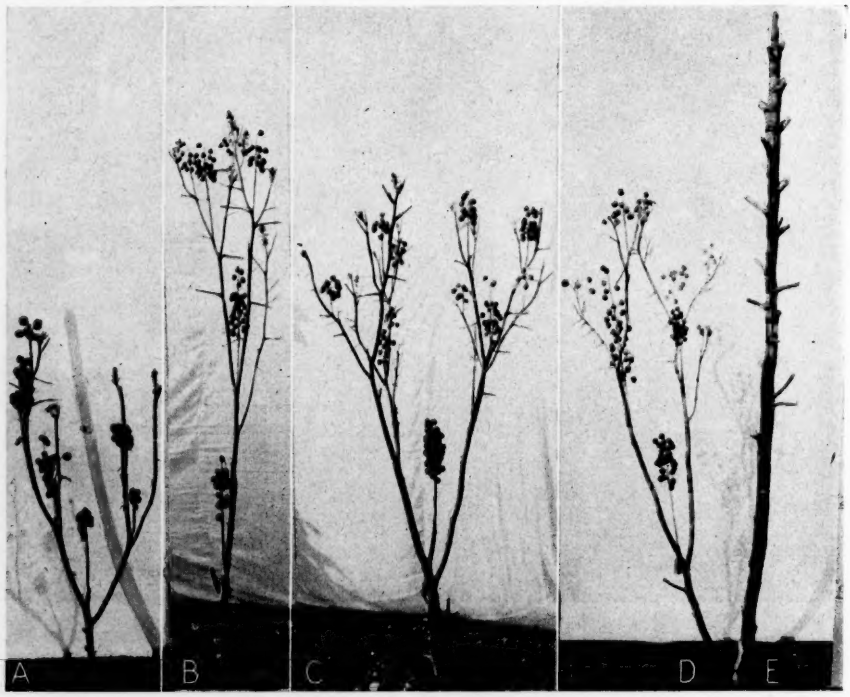
Figure 7

Two plants in F_2 of cross 7 growing in the same hill. On the right the leaves have been removed. The plant with capsules flowered on June 16 at the eleventh node. On August 11, the date of these photographs, the flowerless plant had produced 22 nodes but no flowers.

writer that in all controlled pollinations the F_1 has flowered normally. Although the possibility remains that certain crosses may later be found which have this character in F_1 the designation "hybrid" is not universally applicable. Data are presented below which furnish evidence on the nature of flowerless plants.

In 1943 at the Plant Industry Station F_2 populations* were grown from seven crosses between normal-flowering parents for study of the spineless character. It was noted that the F_2's differed as to the time of flowering of their segregates. In five of these crosses all F_2 plants began flowering in June and July, which is normal for adapted varieties. In the two other crosses the majority of the plants started flowering in June and July, but certain segregates did not flower until August, September or even by mid-October when the plants were killed by frost. The number of plants which failed to flower by frost constituted 11 per cent of one population and 12 per cent of the other. The general nature of the flowerless plants was suggestive of the gigantism character in tobacco, and in 1944 seven F_2's with known parentage were examined more critically for information on this character.

*Seed for these populations was supplied by the Illinois Agricultural Experiment Station where it was produced by the writer in 1942. The original crosses were made by allowing plants of a spineless variant of the U.S.4 variety to outcross with spined plants. Since the spineless character is a simple recessive the presence of spines on any plant in the next generation identified it is F_1. Spined varieties which may have been the male parent in each of the seven crosses were: normal U.S.4; U.S.7 and Arlington, which are similar to U.S.4; and Kansas Common, a distinctly different type.



PARENTS AND HYBRIDS

Figure 8

Plants of cross 3 reduced by the same scale. *A*—The male parent, variety Kentucky 38, flowered on June 21 at the sixth node. *B*—The female parent, variety 227, flowered on June 28 at the ninth node. *C* is an F_1 plant which flowered on June 28 at the eighth node. *D* and *E* are F_2 segregates growing in the same hill. *D* flowered on June 23 at the eighth node, whereas *E*, with 40 nodes, had not produced visible flower primordia by frost on October 16.

Plants in the parental, F_1, and F_2 populations which were grown in 1944 were classified according to earliness of flowering as expressed by the number of nodes below the first raceme.* This classification is based on the observation that the rate of differentiation of nodes is quite uniform in plants not only of the same genotype but of different genotypes. The date of differentiation of each node can be plotted with reasonable accuracy. From these data and by the location of inflorescences, the time when flowers are initiated can be determined fairly accurately. Such a determination facilitates study of the effect of environmental factors on the formation of flowers. The 1944 populations were also classified as to the date of first flowering. In each population the frequency curves of the two classifications differed only in that those for node number were slightly smoother than those for date of flowering. The date-of-flowering character is less desirable in studying the effect of environmental factors on the formation of flowers. Any external stimulus which might result in flower

*In this species the stem is terminated by a raceme. From the base of this raceme an axiliary bud develops into a branch which later presents the appearance of an extension of the main stem.

Table 1.- Parental means and F_2 distributions of earliness as expressed by node number $^{1/}$ in 7 crosses between castor-bean varieties. Means of small populations of F_1 are also given

| Cross | Parent 1 | | Parent 2 | | F_1 | | F_2 distribution/Node number | | |

likely that a particular set of environmental conditions is necessary to induce flowering. This is further indicated by the way in which small numbers of segregates of crosses 1 to 9, inclusive, flowered periodically until frost. Perhaps in these cases one environmental factor or a combination of factors gradually changed, becoming favorable for flower initiation. Factors which change gradually during this period of the growing season include day length, light intensity and temperature. Thus, that which is inherited is probably a flower-regulating mechanism which is controlled by one or more environmental conditions.

Explanation of the mode of inheritance of this response* is made difficult by the continual change in the ratios of flowering to flowerless plants in F_2 as the season progressed. The following facts, however, are significant: (a) the particular gene complex which produces the flowerless character was obtained in F_2 of certain crosses only, (b) the parents and F_1's of crosses which produced flowerless plants in F_2 flowered normally, (c) either of two closely related varieties was invariably a parent in all crosses which produced flowerless plants, and (d) the proportion of flowering to flowerless plants was fairly constant between the seven crosses in which they occurred.

A thorough study of the effect of environmental factors, both alone and in combination, on flowering will clarify the nature of the flowerless condition. Also, an understanding of the effect of each factor on flowering will permit, by the use of controlled environments, intensive study of the inheritance of flowering response to environmental factors such as day length, light intensity, and temperature.

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2. White, Orland E. *Jour. Hered.* 9:195-200. 1918.

*Among the crosses which produced no flowerless plants in F_2, number 14-15 is interesting. In the F_2 distribution of node number a distinct bimodal tendency is evident with the two modes being at or near the values of the two parents. (The date-of-flowering classification produced the same type of curve.) Division of this population into two groups at the low point between the two modes (between node classifications of 12 and 13)yields a ratio of 229:65 which is a good fit to a 3:1 (P=0.20-0.30). This suggests that in this cross. where no flowerless plants occurred in F_2 one major pair of genes was governing earliness.

Research and Social Progress

Permit me a few comments on the first question: Is research essential for social progress? The question tempts me to a blunt remark: Is running essential when you are in a stampede? In other words, with research as a tool available to your competitors can you ignore its power? If you doubt the power of research look about you: Who here is dressed in homespun? Who here breakfasted exclusively on unprocessed foods raised and transported without benefit of meteorology, chemistry, physics and biology? Who got here on his own feet without the aid of airplane, train, subway, taxicab or elevator? Can you, or any one else, stop by fiat or pious resolve the advances of technology? Not without getting left so far behind as to make the words "social progress" a cackling mockery. I suspect that there have been societies and states in the history of the world in which life and human relationships were to the healthy participants as agreeable or more agreeable than life in these modern times is to us. But I am quite sure you wouldn't trade your life for theirs; you like to get well from a ruptured appendix, diphtheria or an acute mania or a rodent ulcer of the face—they couldn't and they didn't. In fact, it is precisely in the field of medical science that I would insist that progress is real. Do you seriously expect progress in the field of drug therapy to come from ignoring the kind of study which has given us our present amazing results in the use of insulin, liver extracts, vitamins, the sulfa compounds and penicillin? — Dr. Alan Gregg. *Science* 101:258. 1945.

And let us not forget genetic selection. Dare we expect continued social progress in a culture wherein genes conditioning superior abilities are less than averagely likely to survive?

INHERITANCE OF COAT COLOR IN SWINE

I. General survey of major color variations in swine.

H. O. HETZER*

IN 1934 an extensive crossbreeding experiment with swine was started by the Bureau of Animal Industry of the United States Department of Agriculture. The primary purposes of this experiment were to make a detailed study of the effects of crossbreeding and to develop new strains which would possess a maximum of the desirable characteristics of their respective parent breeds. Crosses between the following breeds were included in the experiment: Danish Landrace × Poland China, Danish Landrace × Berkshire, Danish Landrace × English Large Black, Danish Landrace × Hampshire, Danish Landrace × Duroc-Jersey, and Yorkshire × Duroc-Jersey. The plan in each case was to produce strains which would resemble the Landrace or Yorkshire in all major details except in color. Instead of the white color possessed by these breeds, the color of the new strains was to be the same as that characteristic of their respective colored parent breeds, thus avoiding the tendency of white pigs to suffer from sun-scald. This objective was to be achieved by the production of relatively large F_2 generations accompanied by suitable backcrosses. Thereafter, the general plan was to mate properly marked segregates back to their white parent breed and to alternate this system of topcrossing with *inter-se* matings between animals saved from the last generation. After a few generations under this plan each new generation was to be produced exclusively by *inter-se* matings between similarly-colored animals.

The purpose of the present and following papers is to present an analysis of the various swine colors, based on a survey of the literature and on the writer's own findings. Some of the data included are hardly satisfactory from the standpoint of particular critical crosses, but the data are in most cases extensive enough to warrant a few well-grounded conclusions.

Color Patterns of Swine

Although considerable work has been done on the inheritance of color in swine, our information on certain phases of the subject is still rather scanty and there is no general agreement as yet as to the factors responsible for some of the major color variations. There are, nevertheless, several colors whose inheritance may be considered to be definitely established. In this connection first place must be given to Wright who in 1918 made a critical survey of the more important literature up to that time.[48] The subject was subsequently summarized by Lush,[21] by Wentworth and Lush,[45] by Kosswig and Ossent[12, 15] and by Kronacher and Ogrizek.[18] More recently (1936) the situation has been treated monographically by Smith and coworkers.[37] The following statements are essentially a summary of what, on the basis of different workers' results and of the writer's own findings, seem most likely to be the essential facts about the inheritance of the major color variations in swine. The results of all the publications reporting data on the color of the progeny of crosses involving different breeds are summarized in Tables I and II. While some of the information in these tables is based on observations that were more or less incidental to some other study, all of the data cited appeared to be sufficiently accurate to merit incorporation into the tables. Statements in the literature based on nothing more

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definite than general impressions are not included.

The "Tortoise-Shell" Patterns

The "tortoise-shell" or extension series of patterns—complete extension of black (i.e. self black), partial extension of black (i.e. black-spotted) and complete restriction of black (i.e. self red) appears to be the best starting point for consideration of the color varieties. There are good reasons for maintaining that the differences between these patterns are primarily due to a series of triple alleles like those of the *E* series in guinea pigs. Thus partial extension as seen in Poland China and Berkshire has been reported to differ from the self red of Tamworth and Duroc-Jersey by one partially dominant factor. (See Literature references 21, 33, 43, 44, 45.)

Self red has likewise been reported to behave as a simple recessive to complete extension as seen in the Hampshire (overlooking the belt) and in the Mule-foot.[2, 8, 20] Complete extension in turn appears to behave as a simple dominant over partial extension.[32] These results, though not absolutely conclusive, show that there are at least two kinds of black, and substantiate the theory of allelism. Incidentally, there is evidence[32] that the black of the Hampshire and the black of the Hanoverian are probably genetically the same. It is also clear that there are minor genetic factors and non-genetic environmental differences which modify the extent and localization of the various black patterns. That such factors exist is clearly shown by the results of Wentworth and Lush[45] who came to the conclusion that the Tamworth possesses a genetic complex more effective for restriction of black than does the Duroc-Jersey, while the Berkshire possesses several factors for extension of black in addition to the main gene for black spotting. These workers even incline toward the view that minor restriction factors may cause genetically black spotted pigs to be phenotypically indistinguishable from non-blacks. Further evidence for the existence of minor factors for restriction and extension of black may be found in the results of Warwick,[43, 44] who obtained both self red and black-spotted pigs from matings between non-black segregates of a Poland China × Duroc-Jersey cross. Warwick has also reported the occurrence of black-spotted pigs among purebred Duroc-Jerseys and Tamworths.

The White Patterns

There are at least four kinds of white patterns. These are (1) the self white of the American, English, German and Scandinavian white breeds, (2) the slaty or dirty white on a dark skin found in the Mangalitza, (3) the white belt possessed by the Hampshire, the Wessex Saddleback, the Essex, and the Hanoverian, and (4) the white responsible for the six white points in the Poland China and Berkshire.

Self White

That the several white breeds are genetically similar seems probable, but there is no definite information on this point except that self white usually behaves as a dominant over all other colors. Thus the Chester White, Yorkshire, Middle White, Large White, Lincolnshire, Edelschwein and Landschwein self whites have been reported dominant over the black of the Berkshire, the Poland China, the Wessex Saddleback, the Hanoverian and the China Black. (See References in Table II.) It is also dominant over the red of the Tamworth, the Duroc-Jersey and the half-red Bavarian, over the dirty white of the Mangalitza, as well as over the agouti pattern of the wild hog. Self white has also been reported dominant over the black of the Large Black and the Hampshire, although these breeds have been found to produce blue grays or blue roans in some crosses. Whether the blue roans reported by Lloyd-Jones and Evvard[20] from Hampshire × Chester White and those reported by Kronacher[16] from crosses of Large Black × Landschwein and Edelschwein, are genetically similar to the Sapphire hog, described by McLean[22] is not certain. However, such evidence as the writer has shows that the

Table 1 Summary of data on color of F1 progeny reported in the literature from crosses of black x black and black x red. References to the literature are given by numbers in parenthesis

Parent breeds →	Berkshire (black, white points)	Poland China (black, white points)	Hampshire (black, white belt)	Uncverian (black, white belt)	Large Black (solid black)	Ruhr-Sand Dog (solid black)	China Black (solid black)
China Black (solid black)	solid black (b) (d) (11)	solid black (b) (d) (11)	solid black to belted black (26 pigs) (a) (11)				
Large Black (solid black)	solid black, black with white spots (about 12 litters) (5)						
Uncverian (black, white belt)	black with white belt(d) (9) black with white belt(c) (26)				black with white belt(d) (9)		
Hampshire (black, white belt)	black with white feet to black with white belt (32)			black with white belt (9-1 a) (32)			
Duroc-Jersey (solid red)	red with black spots(c) (39,40)	red with black specks (c) (30) red to red, black spots (132 pigs)(d) (44) red with black spots(c) (46)	black with white belt(c) 39,40) black with white belt (479 pigs) (e) (20) black with white feet to black with white belt (17 pigs)(e) (2)			solid black (about 250 pigs)(e) (6)	black, reddish tan, some with stripe (11) (6 litters)(e)
Tamworth (solid red)	red with black spots (c) (39,40) red with black spots (c) (55) red with black spots, solid red (10 pigs) (21,46)		black with white belt (c) (39,40) black with white belt (c) (55) black with white belt(d) (55)				
Half-red Bavarian (= red-white)	red with black spots(d) (12)				black with white points, reddish stripes (several litters)(c) (16)		

a) Cross made only with North China Blacks
b) Cross made with North and South China Blacks
c) Information based on several observations
d) Number of pigs not given
e) Cross carried to F_2 and/or backcross generation

appearance of blue roans in the F_1 generation of crosses between the Danish Landrace × Hampshire is due to a gene possessed by the Landrace rather than to genes brought in by the Hampshire. This gene appears to dilute black to blue roan in animals carrying the gene for full extension of black, and to sandy or white in case only the gene for partial extension is present. As regards the inheritance of self white, Wright[48] suggested that self white is determined by two major genes, that for dilution of red being dominant, and that for restriction of black being either dominant or recessive. Wentworth and Lush,[45] on the other hand, state that white probably is dependent on a single dominant gene. Whether this is a dilution factor for red similar to the one suggested by Wright or whether this gene acts as an inhibitor of both red and black is not mentioned by these workers. In the early 1930's, Kosswig and Ossent[12,13,14] suggested that white is determined by at least two complementary dominant factors. Before that, Kronacher[16,17] had suggested that the differences between white, the agouti pattern of the wild hog, black and red were due to a system of multiple alleles. After Kosswig and Ossent's reports appeared he stated[18,19] that his results could be explained by their hypothesis.

It is beyond the scope of this paper to discuss the evidence in support of the various hypothesis cited above except to note that all of the published data, with but a few doubtful exceptions, can be as readily explained on the hypothesis that self white is primarily determined by a single dominant gene. This conclusion is clearly substantiated by the writer's own findings which show that white is due to one major dominant gene, capable of inhibiting either red or black color. Such evidence as the writer has also shows that the gene which in the case of the Landrace × Hampshire hybrids modifies black to blue roan probably is an intermediate allele of the series primarily responsible for the production of color. As in the case of the "tortoise-shell" patterns, the self white and blue roan patterns undoubtedly are

Table II. Summary of data on color of F_1 progeny reported in the literature and by the author from crosses of white breeds with other breeds, including the wild hog. - References to the literature are given by numbers in parentheses.

Parent breeds ⟶ / ↓	Chester White (solid white)	Yorkshire (a) (solid white)	Lincolnshire (solid white)	Improved Landschwein (solid white)	Edelschwein (solid white)	Danish Landrace (solid white)	Mangalitza (dirty white)	Wild hog (agouti)
Berkshire (black, white points)	white, white with black spots (c) (53)	white (c) (38) solid white (38 pigs)(f)(56) solid white, rarely black spotted (c) (33) white (6 litters) (32)	white (10 pigs) (42)	white (c) (16) white (19 litters)(f) (32)	white with blue spots (2 litters) (9) solid white (c) (26) white (14 pigs)(f) (17)	white, white with blue spots (69 pigs) (c) (f)	white with black spots, 1. stripes (22 pigs)(f) (41,42) wild color with black spots (8 pigs) (12)	wild color wth black snots stripes (17 pigs) (21 ,45) wild color with black spots (26 pigs)(f) (32) wild color with black spots, black with white spots(11 pigs) Used wild-colored hogs of mixed ancestry. (13)
Poland China (black, white points)	white, white with blue spots (50 pigs) (c) white (c) (20)	solid white (d) (34) white (c) (38) white (c) (46) solid white (77 pigs) (36)				white, white with blue spots (142 pigs) (c) (f)		
Hampshire (black, white belt)	blue roan, white belt(1 litter) (20)	white (d) (35)		white with greyish blue spots (26 pigs)(f) (32)		white, white with blue spots, blue roan (65 pigs)(c)(f) (used solid black Hamp.)		
Wessex Saddleback (black, white belt)		white with blue spots (770 pigs) (29)						
Hanoverian (black, white belt)		white (10 pigs)(f) (32)			white (c) (9) white (1 litter)(f) (16) white with skin spots (17 pigs) (32)			black with white belt, no stripes (d) (9) black with white belt, no stripes (d)(f) (10) black with white belt, brown stripes (9 pigs) (32)
Large Black (solid black)		white with blue or black spots (c) (6) white with blue or black spots, rarely black with white points (c) (37)	white with blue spots some with 1. stripes (10 pigs)(f) (42)	white, white with blue spots, blue gray with or without 1. stripes, white with black spots, black with white belt or black with white points (55 pigs)(f) (16,18)	white (c) (9) white, white with blue spots, blue gray, some with white belt(28 pigs) (f) (16,18)	white, white with blue spots (90 pigs)(c)(f)	solid black, some with brown stripes (18 pigs) (f) (4,5) black, also dark wild color (9 pigs) (31) black, gray 1. stripes (6 pigs)(f) (41,42)	wild color, black with 1. stripes, white with black spots (several litters) (used wild-colored hogs of mixed ancestry) (12)
China Black (1) (solid black)	white with blue spots (1 litter) (11)	white with blue spots (d) (11)						
Duroc-Jersey (solid red)	white, reddish tint (c) (46)	white, reddish tint(c) (33) white, reddish tint(c) (46) white, white with blue spots, reddish tint (109 pigs)(c)(f)				white, white with blue spots, reddish tint (218 pigs)(c)(f)		
Tamworth (solid red)		white with blue spots (11 pigs) (38) white, reddish tint, 1. stripes (d) (34,35) white (12 pigs) (9) white, reddish tint(c) (33)			white (c) (9) white, white with reddish spots (37 pigs) (17 18) (also used Middle White)	White with varying amounts of black skin pigment (63 pigs) (47)	white, reddish white, 1 stripes (8 pigs)(f)(41,42)	wild color(1 litter)(f) (38) wild color (c) (9) wild color, reddish tint (38 pigs)(f) (21, 45)
Half-red Bavarian (red-and-white)				white, some with reddish tint (11 litters)(f) (16)	solid white,1. stripes(d)(10) white (about 250 pigs)(f)(16)			wild color(2 pigs) (12)
Wild hog (agouti)		white with grey spots (2 pigs) (f) (7)		white, white with black, 1. stripes (7 pigs) (9) white with 1. stripes (several litters) (17) white with 1. stripes, skin spots (23 pigs) (32)	white with 1. stripes, blue spots(19 pigs)(f) (9) white with 1. stripes (several litters) (17)		wild color, wild color with black spots (several litters) (used wild-colored hogs of mixed ancestry) (12)	
Mangalitza (dirty white)		white, white with yellowish spots and 1. stripes(84 pigs) (f) (5)	white, light 1. stripes (13 pigs) (f) (42)					
Improved Landschwein (solid white)		white (41 pigs)(f) (32)						
Danish Landrace (solid white)	solid white (53 pigs)(e)	solid white (27 pigs)(e)						

a) This includes Middle White and Large White
b) Illustrations of China Blacks are given by F.W.Phillips in the December 1944 issue of this Journal
c) Information based on general observations
d) Number of pigs not given
e) Data obtained by the Bureau of Animal Industry,U.S.D.A.
f) All except those from crosses of C.W.x P.C, C.W.x D.L. and Y x D.L. are presented elsewhere in this series
g) Cross carried to F_2 and/or backcross generation

affected by minor genetic factors, a conclusion supported by the fact that homozygous self whites occasionally show varying numbers of skin spots, occasionally accompanied by the presence of black or red hairs. Heterozygotes produced by such animals, on the other hand, are sometimes completely self white.

The White of Mangalitza

As noted above, the Mangalitza breed is characterized by a slaty or dirty white color on a dark skin. It is also characterized by the presence of black pigment on the snout, cloves, eyelids and the tip of the tail. Moreover, the young are born with longitudinal stripes which usually disappear at four to five weeks of age. The pattern of the adult has been reported recessive to the black of the Large Black, to black of the Berkshire and to the white of the Yorkshire and Lincolnshire. (See Literature references in Table II.) In crosses with the Tamworth, Teodoreanu[41] found red to be at least partially dominant in F_1, while reds and whites occurred in F_2 as well as in backcrosses to Tamworth and to Mangalitza.[42] The striping pattern of the young, on the other hand, appears to be dominant over black of the Large Black and of the Berkshire. It is also dominant in crosses with Tamworth and Yorkshire. (See Literature references in Table II.) In F_2 from this latter cross there were both whites and whites with black spots,[5] while blacks and whites segrated in F_2 of crosses with Berkshire and Large Black.[42] Constantinescu[5] suggests that the white of the Yorkshire differs from the Mangalitza white by a single dominant gene and that the latter possesses a distinct dominant gene for immature striping which generally is hypostatic to dominant white. To account for the appearance of solid blacks in the F_1 of some crosses with the Large Black, Constantinescu[5] further suggests that some Mangalitzas are heterozygous for a dominant dilution factor which is necessary to produce stripes. Kosswig and Ossent[12] previously concluded that the white color of the Mangalitza differs from all other colors by a single recessive factor and that the striping pattern is determined by the same dominant factor possessed by the wild boar.

Belted Patterns

The white belt characteristic of the American Hampshire, its English cousin, the Wessex Saddleback, the Essex and the Hanoverian evidently is determined by the same or similar factors.[30,32] However, the pattern of these breeds is subject to a great deal of variation, for solid whites as well as solid blacks have been reported both in the Hampshire[35] and the Wessex Saddleback breeds.[29] Whether such opposite extremes are due to accumulations of different modifying factors is not certain but there can be no doubt that such factors exist. It is also evident that the variations commonly observed in the width of the belt are at least partly environmental in nature. By crossing the Hampshire with the Tamworth, Simpson[35] found that the belt of the former could be transferred to red hogs, a result subsequently confirmed by Bushnell.[2] The presence of belting factors as reported in some Tamworths,[25] in Duroc-Jerseys[27] and in American Herefords,[1] clearly falls in line with the hypothesis of Wright[48] that the Hampshire belt is determined by factors which act on the distribution of either black or red color. Nordby[27] assumes that the belting pattern found in some Duroc-Jerseys is genetically the same as that in the Hampshire, a view shared by Bushnell.[2] It is not yet certain how the belting pattern behaves in crosses with some breeds, but the available evidence shows that there is a tendency to dominance in the F_1 generation in crosses involving the Tamworth,[9] the Duroc-Jersey,[2] the Berkshire[32] as well as the wild hog.[10,32] In addition, belted pigs have been reported among the progeny of Duroc-Jersey $\times$ Yorkshire and Tamworth $\times$ Chester White crosses[40] and of Tamworth $\times$ Yorkshire,[35] as well as among the progeny of solid black hogs.[28]

According to Spillman,[40] the belting pattern cannot be determined by less than two factors, for solid black individuals

have belted offspring and vice versa. This result has been confirmed by Olbrycht[28] who concluded that the belting pattern is determined by several factors. More recently Bushnell[2] has reported that the Hampshire belt depends on a dominant gene for white and one main gene for extension of white. He also suggested that the gene for white and the gene for black color are linked with a cross-over value of approximately 41 per cent.

White Points

The fourth kind of white which remains to be discussed is that responsible for the six white points on the feet, face and tail of the Poland China and Berkshire. In an extended form, this type of white also appears to account for the irregular white spots of the Spotted Poland China. As already noted, the whole pattern probably is influenced by several factors, for even among purebreds there is some variation in the proportion of black and white present, and occasionally some of the white areas have a distinct reddish tint. There is no question that the white exhibited by the above breeds differs genetically from that of the Hampshire, but as yet there is no agreement about its mode of inheritance. Wright[48] after examining the results of several earlier workers[33,36,38] advanced the hypothesis that the Berkshire and Poland China breeds are genetically sandy hogs with black spots. Through selection of minor factors for extension of black and dilution of red they have changed into black breeds with white points. Postulating the same sort of foundation for the solid red breeds (Duroc-Jersey and Tamworth), Wright further suggested that the solid red of these breeds has come about through selection of minor factors for intensity of red and restriction of black.

Lush[21] and Wentworth and Lush[45] on the other hand, maintained that Berkshire white is due to recessive alleles of two major genes possessed by the Duroc-Jersey, either one of which produces sandy, and both together produce red. To account for an excess of whites and a deficiency of sandies among their black-carrying F_2's these workers assumed further that there is a dominant gene linked to black which dilutes sandy to white in the presence of one of the genes for sandy. One point of considerable importance in this connection was the tendency for extension of black to be associated with dilution of red, a result previously observed by Severson[33] in Berkshire $\times$ Duroc-Jersey crosses.

Not only can these latter results be as readily explained by a physiological interrelation between the processes of forming black and red pigment as suggested by Wright[48] but there is also evidence that the factorial interactions postulated by Wentworth and Lush fail to explain the results obtained by other workers. If the red of the Duroc-Jersey were really due to the cumulative action of two dominant genes, it should be impossible for dilute reds to appear in a backcross to the Duroc-Jersey. On this point Wentworth and Lush had no evidence, but several workers[2,8,43] have reported the occurrence of various kinds of dilute reds among the backcross progeny of crosses similar to those of Wentworth and Lush. These results indicate that the white of Poland Chinas and Berkshires is an extreme variation of red modified to sandy or white by two or three more or less dominant dilution factors.

Red of Tamworth and Duroc-Jersey

If the above hypothesis is correct, the self red of the Tamworth and Duroc-Jersey must be looked upon as being due to a combination of a recessive gene for restriction of black with two or three partially recessive intensity factors for red. While the production of reds (with black) reported by Wentworth and Lush[45] in the F_1 generation of crosses with pure Berkshire would hardly be expected on this latter hypothesis, there is ample evidence that recessive intensifying factors exist. Not only can the F_2 and backcross data of Wentworth and Lush be explained on this basis, but the combined results of other workers (including those of the writer) practically rule

out any other hypothesis. In order to reconcile the results of Wentworth and Lush with the hypothesis of recessive intensity factors, it appears that the same sort of physiological interrelation between the processes of forming black and red pigments as postulated for some of their F_2 data can be evoked to account for the apparent dominance of red in the F_1. The fact that their Berkshire × Tamworth and Berkshire × Duroc-Jersey F_1 hybrids had very little black as compared with the amount of red present, gives ample support to this view if we remember that in the case of their black-carrying F_2 pigs there was a tendency for black to occur in larger amounts in the presence of white than in the presence of red. As regards the relation of red to other colors, there is evidence from the results of this experiment that both the black of the Large Black and of the Hampshire, and the white of the Landrace and the Yorkshire, are epistatic to red. Like the Poland China and Berkshire, the Landrace and Yorkshire appear to possess two or three cumulative partially dominant genes for dilution of red, lacking in whole or in part in Hampshires and Large Blacks. That these genes for conditioning the dilution and intensity of red are inherited independently of the other color genes appears probable, but additional data are necessary to confirm this particular point.

The Wild Hog

The color of the wild hog is usually considered to correspond to the agouti of rodents except that the wild hog has a darker and more slaty appearance. Furthermore, at birth wild hogs have longitudinal stripes instead of being self colored, and there is a tendency for the underline to be lighter than is usual among the domestic breeds. According to Wentworth and Lush[45] it is probable that these characteristics of the wild hog are pleiotropic manifestations of a single gene. Yet there is evidence that crosses not involving the wild hog may produce striped pigs which subsequently fail to show the adult agouti pattern.

Whatever the basis for this apparent independence of juvenile striping and the adult agouti pattern, both components have been reported dominant over the self red of the Tamworth, the black of the Berkshire and the Large Black. Both are recessive to the self white and the white belting patterns. (See Literature references in Table I.) However, wild × white hybrids have been reported to show distinct longitudinal stripes, which resemble a "ghost pattern" in appearance. That the wild pattern may be determined by more than one gene is indicated by the fact that the black of the Hanoverian has been reported completely dominant in some crosses[9,10] and more nearly recessive in others.[32] There are also F_2 and backcross data which show clear-cut segregation of the wild color pattern as manifested in different crosses. Thus Spillman[38] reported that the red of the Tamworth differs by a single factor from wild color, a conclusion confirmed by Wentworth and Lush.[45] As regards the relation of the wild color to black, Schmidt and Lauprecht[32] record crosses of wild × Berkshire which indicate either that the former has a gene in the extension series which tends to restrict black or that the partial extension gene present in the Berkshire is modified by the agouti gene carried by the wild hog. Haecker[10] reported on a cross of a wild hog with Hanoverian, wherein the F_1 was black and the F_2 showed segregation into four black to two wild.

These results support the concept of a single gene difference between black and wild, but do not thereby preclude other explanations. In this connection, attention should also be called to Kosswig and Ossent's conclusion[12] that the wild hog possesses a hypostatic gene for black linked to a gene for wild color, a formulation needing confirmation as many of their arguments do not appear to be altogether convincing. The reports of Fröhlich,[9] Kronacher[17] and Schmidt and Lauprecht[32] on wild × self white crosses indicate that only a single gene-difference is involved but again the available evidence is not extensive

enough to permit a final conclusion as to the genetic nature of the wild color pattern.

In addition to the above colors, several not found as standard breed patterns, appear to be distinct enough to be mentioned at this time. One of these is the sepia color reported by McPhee and coworkers.[23,24] This appears to be a dilute black and probably differs from the black of the Poland China by a single recessive dilution factor. The other patterns which remain to be mentioned are the red roan, red-and-white, red-and-sandy, sandy-and-white and red-sandy-and-white patterns. These patterns occur rather frequently among the descendants of crosses involving the red breeds both in the presence and absence of black. While these patterns are generally considered to represent different grades of dilution of red, further work is needed to establish this point.

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